THE USE OF SPIDER SILK IN THE INITIATION OF NEST-BUILDING BY WEAVER ANTS (FORMICIDAE: FORMICINAE: *POLYRHACHIS*)

PETER D. DWYER AND DANIEL PATRICK EBERT

Dwyer, P.D. & Ebert, D.P. 1994 12 01: The use of spider silk in the initiation of nest-building by weaver ants (Formicidae: Formicinae: *Polyrhachis*). *Memoirs of the Queensland Museum* **37**(1): 115-119. Brisbane. ISSN 0079-8835.

Field and laboratory observations of *Polyrhachis doddi* and *P. pilosa* in southeastern Queensland, Australia, showed that spider silk is used commonly in nest-building, is used often instead of larval silk when workers initiate nests or extend pre-existing nests and, at least in the laboratory when larvae are unavailable, may be used to build entire nests. Founding queens of both species also used silk from spiders when initiating nests. In nearly all cases, silk came from shelters of spiders such as salticids and clubionids. Silk from spider webs was rarely used. The functional and evolutionary significance of the use of spider silk are discussed. ☐ *Polyrhachis, weaver ants, nest-building, spider silk, founding queens.*

Peter D. Dwyer & Daniel Patrick Ebert, Department of Zoology, The University of Queensland, Brisbane, Queensland 4072, Australia; 27 August 1994.

Many species of the Old World formicine genus *Polyrhachis* use silk that is produced by their own larvae in the construction of nests (Hölldobler & Wilson, 1983, 1990). This behaviour is particularly evident in arboreal species of several subgenera (e.g. *Cyrtomyrma*, *Myrmatopa*, *Myrmhopla*) which build pocket nests of silk on tree trunks and the undersides of leaves or which use silk to join the leaves of various trees and shrubs (Dorow & Maschwitz, 1990; Dorow et al., 1990; Kohout & Taylor, 1990; Ofer, 1970; Yamauchi et al., 1987). In nests of the latter kind, as made by Australian *Cyrtomyrma* species for example, interior walls are covered by a thin, tough layer of silk and exterior portions, joining leaves, may be strongly reinforced by debris. At completed nests, neither the larval silk nor the ants inside are visible.

Nest-weaving, as described in *Polyrhachis* species and in other weaver ants, poses two related problems which have not received attention. First, in the earliest phase of colony formation, queens do not have larvae and, hence, lack access to larval silk with which to initiate nests. Secondly, initiation of new nests by workers requires transport of larvae from sheltered sites to open situations where they may be exposed to both potential predators and exigencies of weather. One of us, for example, has observed substantial predation by the skink *Lampropholis delicata* upon *Polyrhachis* larvae during a mass movement from one arboreal nest to another. The skinks attempted to retrieve larvae from *Polyrhachis* workers while avoiding direct contact with the workers themselves. Chemicals released by the ants are a powerful deterrent to these lizards (cf. Bellas & Hölldobler, 1985).

In the green tree ant, *Oecophylla*, founding queens do not make nests; these ants are cryptically coloured and they rest, and commence rearing their first broods, in exposed positions on the undersides of leaves (Dorow et al., 1990; Peeters & Anderson, 1989; Wheeler, 1915). Again, when *Oecophylla* workers initiate nests, the security of exposed larvae is ensured firstly by the recruitment of many workers that may defend those larvae and, secondly, by the rapidity with which nests may be built (Hölldobler & Wilson, 1990). Neither of these options is available to species of *Polyrhachis* (*Cyrtomyrma*) which are black and conspicuous and do not recruit large numbers of workers to new nest sites. In this paper we report that, in two Australian *Cyrtomyrma*, a common solution to potential problems associated with initiating nests entails the use of silk produced by spiders as a substitute for that produced by ant larvae. The use of alternative silks by these weaver ants has not previously been recognised. Indeed, Dorow et al. (1990: 184) wrote that, in the laboratory, the Southeast Asian *P. muelleri* did not accept silk from spider webs. Our observations have significance for both functional and evolutionary interpretations of weaving behaviour in *Polyrhachis*.

STUDY AREA AND METHODS

In southeastern Queensland, *P. doddi* and *P. pilosa* are abundant species of arboreal weaver ant. Both make nests in many different species of plants of diverse leaf form. For example, 60 nests of these species censused in May 1993 at the Mt Coot-tha Botanic Gardens, Brisbane, were located in 30 plants of 23 species in 10 families (17 nests in Myrtaceae, 16 in Arecaceae and 12 in Theaceae; C. Hunter, pers. comm.). Nests of these species are also found, among other places, in hollows of dead *Plumeria* branches, leaf bases of bromeliads, petioles of climbing *Philodendron*, rolls of *Eucalyptus* bark and a variety of artificial sites (e.g. plastic buckets and covered plant pots suspended in trees).

From January 1993 to February 1994 we made opportunistic observations of nest-building by *P. doddi* and *P. pilosa* in suburban gardens, and at the St. Lucia campus of the University of Queensland, Brisbane. From September 1993 to February 1994 we also made observations of nest-building by captive *P. doddi*. Groups of 25 to 55 workers were established in 28 × 21 × 7cm plastic trays that were isolated by moats. (In the field *P. doddi* and *P. pilosa* initiate nests using groups of less than 20 workers). The trays were weighted with sand, sticks were provided as walkways and plant debris (very small leaves and broken seed capsules of *Melaleuca* and *Leptospermum*) was supplied. Each tray was provided with a small artificial tree, less than or equal to 30cm high, consisting of two or three branches of 'silk' (rayon) Ficus. Artificial trees were made in such a way that parts of some leaves of different branches were 0.5-1.0cm apart but not in contact. Leaves were aligned more or less vertically. Fibres from the 'silk' plants were not used in construction of nests. Sampled nests were from *Buckinghamia celsissima* and *Casuarina littoralis*. Ants were fed on a mixture of egg and honey according to the recipe in Hölldobler & Wilson (1990: 632). All observations were at temperatures between about 15 and 30°C.

RESULTS

FIELD OBSERVATIONS

Spider silk is often visible in the walls of new *P. pilosa* and *P. doddi* nests before these walls are covered with debris. Spider silk is sometimes included with plant fragments, insect frass and fragments of chitin as part of the outer, protective cover of nests. Workers of both species have been seen harvesting silk from shelters built by spiders and transporting it to nest sites. In the field, we have not seen larvae being used in open situations during the earliest phase of nest-building.

P. pilosa have been observed to initiate nests without the aid of larvae on at least six occasions. These nests were made in or between leaves of *Syzygium luehmannii*, *Backhousia citriodora*, *Howea forsteriana*, *Mangifera indica*, *Caryota mitis* and *Brachychiton acerifolium*. In the first three cases, 10 to 20 ants used silk from shelters of unidentified spiders; they worked for two to four days to provide partially enclosed spaces before carrying larvae to the nest sites. The fourth nest was initiated, but not completed, in a dead, furled leaf of *Mangifera indica* caught in the abandoned web of a *Nephila* (Araneae). Ants manipulated the web to increase leaf curvature and attached debris to strands of web that joined the edges of the leaf. After three days, when a partial shelter had been formed, one larva was carried to the new nest. The fifth nest, built by a founding queen, was in a rolled leaflet of *Caryota mitis*; this leaflet had originally housed a spider shelter and silk from the shelter, together with a little attached debris, formed the exposed walls of the nest. The sixth nest was initiated by *P. pilosa* workers that used waxy filaments secreted by a coccid (Homoptera) to join the leaves.

Sites chosen for building nests in two large stands of *Phoenix roebelenii*, one stand occupied by each species of *Polyrhachis*, contained shelters of salticid and clubionid spiders, including those of *Opisthoncus* and *Clubiona*. These spider shelters were spun between adjoining leaflets of fronds and, particularly with the tightly woven shelters of salticids, had the outcome that the leaflets were pulled together and overlapped for part of their length. *Polyrhachis* workers with larvae cannot achieve this rearrangement of the thick, stiff leaflets (personal observations). Because the orientation of leaflets at nearly all *Polyrhachis* nests in these palms matched the orientation produced by spiders we think that most observed nests ($n = 12$) were initiated at spider shelters. At one *P. doddi* nest the 16cm long walls that joined two leaflets were made entirely of silk from the shelters of spiders. Workers were seen harvesting silk from a nearby salticid shelter and carrying it to the nest.

Two large, galleried nests of *P. doddi* in *Casuarina cristata* and one small nest in *Syzygium luehmannii* were extended by workers that carried silk from spider shelters to the sites; larvae were not used until the extensions were well underway and provided covered areas within which workers could effectively hide the larvae from view. Four nest sites used by founding queens of *P. doddi* were established at spider shelters in furled leaves of *Tupidanthus calyptratis* and *Schefflera actinophylla*. The queens had teased apart the spider shelters and attached some debris to make open nests that, in two cases, were used for more than a month by up to eight queens. Founding queens of *P. doddi* have been often observed sheltering under or inside palm leaflets which had been either folded by spiders making silk shelters or rolled by the larvae of palmdarts (*Cephrenes*). In the latter case, abandoned *Cephrenes* shelters that had subsequently been used by spiders were preferred by the queen ants. When using temporary shelters during the daytime, *P. doddi* queens are often in contact with the silk of spider shelters, either between leaves or in leaves that have been curled by the spiders.

LABORATORY OBSERVATIONS

In mid-September 1993, three groups of workers, each with access to an artificial tree, were provided with silk from old, abandoned salticid and clubionid shelters. Three additional groups were provided, respectively, with spider web and egg cases (the latter from *Zosis* sp.[Uloboridae: Araneae]), cotton wool and five large larvae. All groups, except that with cotton wool, initiated nest-building in late September and continued intermittently through October and November. In late November the group with larvae and two of the groups with salticid and clubionid shelters had completed building nests between leaves of the artificial trees. After several aborted attempts, the group with web and *Zosis* egg cases used silk from the egg cases to complete a small nest beneath a stick on the floor of the tray.

On December 24, 1993, three groups of workers in artificial trees were provided with silk from recently built salticid and clubionid shelters. On February 8, 1994, these groups of ants had completed two-thirds, one-quarter and one half, respectively, of the areas of wall needed to enclose each nest. The trial was then terminated because, in two groups, larvae produced by workers were approaching the size at which they might produce silk.

Donor colonies of *P. doddi*, housed in the laboratory, also built nests using silk from salticid and clubionid shelters. These large groups, with queens and larvae, initiated nests with spider silk more often than with larval silk. One group took apart, and reused, the entirety of an old nest; in another goup, with about 200 workers, ants began harvesting spider silk 10 minutes after the silk was provided.

In the laboratory, *P. doddi* workers harvested silk from spider shelters by tearing at the shelter and pulling and biting portions free. They did not cooperate in this activity. Often, however, when the load had been carried to the nest site it was attached to an artificial leaf at places which had been moistened by fluid from the mouth of another worker. Sometimes the ant that carried the spider silk waited as the other ant moistened the leaf and, on a few occasions, the latter ant retrieved the silk from the former and attached it to the leaf. This behaviour differs from that of *Polyrhachis muelleri* which, when using old larval silk or cotton wool, glued the material into place with a droplet from the tip of the gaster (Dorow et al., 1990).

P. doddi seldom isolated single fibres from the masses of spider silk that were transported to nest sites. They teased each load apart to produce a flocculent mass of fibres. These were either built out from one leaf surface in layers or stretched between two leaves by manipulating with mandibles and anterior legs. Plant debris was inserted into the mesh of fibres rather than being stuck onto it as occurs when larval silk is used. In two cases, when a vertical wall was built from spider silk the weight of attached debris contributed to pulling silk fibres from the upper to the lower leaf edge. In the laboratory, all *P. doddi* nests built between vertically aligned leaves were commenced at the bottom, proceeded through arching, vertical walls and were completed by covering the top of the chamber and making an entrance. Nests made in analogous situations in the field were also built in this sequence.

Nests made entirely from spider silk were not as strong as those that incorporated larval silk. The latter material provides a firm base to which debris can be attached with some precision. Walls constructed from spider silk lack rigidity and cannot support a complete cover of plant debris without collapsing. Nor can workers construct the characteristic well-formed circular entrance to the nest without access to larvae. The quality of laboratory built nests, made from spider silk alone, is such that they would fall apart rapidly if exposed to even moderate rain or wind.

DISCUSSION

Field and laboratory observations of *P. doddi* and *P. pilosa* show that silk produced by spiders is used very commonly in nest-building, is used often instead of larval silk when workers initiate nests or extend pre-existing nests and, at least in laboratory settings, may be used to build entire nests. In all these cases, *Polyrhachis* workers actually manipulated or transported spider silk in the process of nest-building. We are not dealing merely with the use of 'preformed shelters of spiders and caterpillars' which Maschwitz et al. (1991: 308) reported for an arboreal dolichoderine ant (*Technomyrmex* sp.); they commented that sites of these kinds might be easily 'misidentified as nests produced by the ants themselves'. Founding queens of both *P. doddi* and *P. pilosa* have been also observed to use silk from spiders when initiating nests. Indeed, there appears to be a close association between *P. doddi* queens and abandoned spider shelters.

Our observations suggest that silk from spider shelters is much more likely to be used by *P. doddi* and *P. pilosa* than silk from spider webs. Nests of these species are, however, often built where leaves are tangled in web and we have sometimes seen *P. pilosa* tugging at and manipulating silk in webs that were occupied by spiders. Dorow et al. (1990) reported that 'silk from spider webs' was not accepted by nest-building *P. muelleri*; it is possible, however, that this species would accept other forms of spider silk.

Arboreal *Polyrhachis* species do not display the highly cooperative nest-building behaviour seen in *Oecophylla* where large numbers of ants, recruited to favourable sites, form lines or hanging chains and bend or manoeuvre leaves such that larval silk can be used to hold those leaves in their new positions (Hölldobler & Wilson, 1977, 1990). Rearrangement of leaves observed at many arboreal nests of both *P. doddi* and *P. pilosa*, especially in stiff-leafed plants (e.g. some palms), could not be achieved by the ants themselves, either with or without assistance from larvae. Most of these nests will have been initiated at places where leaves had been already repositioned through the actions of other animals, usually by spiders spinning silk shelters. By contrast, in various Myrtaceae species, *Polyrhachis* workers preferentially build nests in young leaves which are easily bent into unconventional positions; even in these plants, however, our observations were only of nests initiated or extended using spider silk and not larval silk. Dorow & Maschwitz (1990) described rapid recruitment of *P. hodgsoni* workers and larvae to potential nest sites on broad-leafed bamboo (*Gigantochloa* and *Schizostachyum*); ants opportunistically exploited occasions when changes in turgor caused edges of a leaf to move towards each other. These authors also reported that nests of *P. hodgsoni* were also built in leaves that had been rolled by spiders, orthopterans, caterpillars and climbing plants. At exposed sites, where larvae would be easily visible, *P. doddi* and *P. pilosa* usually commence nest-building without recruiting larvae to the site.

With specific reference to *Oecophylla*, Hölldobler & Wilson (1990: 618) argued that weaving behaviour freed ants from 'the spatial limitations imposed on species that must live in beetle's burrows, leaf axils ... and other preformed vegetation cavities' (see also Dorow et al., 1990, on *Polyrhachis* and Maschwitz et al., 1991, on *Dolichoderus*). Dorow et al. (1990: 188) commented further that in arboreal *Polyrhachis*, as in *Oecophylla*, weaving behaviour facilitates polydomy which, itself, may be beneficial in reducing distances to food sources, providing alternative nest sites after catastrophes and, perhaps, facilitating defence of foraging areas. Observations reported here both reinforce and extend earlier conclusions. Use of spider silk as an alternative to larval silk will increase the availability of nest-building sites to *P. doddi* and *P. pilosa* and allow assessment of the quality of potential nest and foraging sites by workers prior to incurring the costs of transporting larvae. Potential costs to larvae that would arise from silk production and risks associated with exposure will be also reduced when silk from spiders is used to initiate nests. And, further, our observations show how founding queens, which lack access to larval silk, may initiate arboreal nests.

Hölldobler & Wilson (1990) considered that the exploitation of larval silk by workers released weaver ants from their ancestral dependence upon a variety of preformed vegetation cavities. This opinion is difficult to accept if, as Dorow et al. (1990) suggested and our observations imply, the failure of *Cyrtomyrma* species to make cocoons is independent of the amount of silk contributed to nest-building. The behaviour of both workers and founding queens of *P. doddi* and *P. pilosa* suggests that use of spider silk could have been a precursor to use of larval silk in the origin of nest-building by at least some groups of arboreal *Polyrhachis*. Answers to questions regarding the origins of these behaviours will require comparative knowledge of silk production in the genus as a whole and knowledge of the extent to which silk production is under worker or larva control.

ACKNOWLEDGEMENTS

We thank Rudy Kohout, Geoff Monteith, Val Davies and Yvonne Ross for help with the identification of *Polyrhachis*, other insects, spiders and plants, Chadden Hunter for providing data on nest composition and Ross McKinnon for authorizing censuses at the Mt. Coot-tha Botanic Gardens. Special thanks to Jeffrey Willmer for frequent access to his garden, plant identifications and a keen ability to locate ants in hard-to-see places. Discussion with Simon Robson rekindled an interest in *Polyrhachis* and Monica Minnegal commented on the manuscript.

LITERATURE CITED

BELLAS, T. & HÖLLDOBLER, B. 1985. Constituents of mandibular and Dufour's glands of an Australian *Polyrhachis* weaver ant. Journal of Chemical Ecology 11: 525-538.

DOROW, W.H.O. & MASCHWITZ, U. 1990. The *Arachne*-group of *Polyrhachis* (Formicidae, Formicinae): Weaver ants cultivating Homoptera on bamboo. Insectes Sociaux 37: 73-89.

DOROW, W.H.O., MASCHWITZ, U. & RAPP, S. 1990. The natural history of *Polyrhachis (Myrmhopla) muelleri* Forel 1893 (Formicidae Formicinae), a weaver ant with mimetic larvae and an unusual nesting behaviour. Tropical Zoology 3: 181-190.

HÖLLDOBLER, B. & WILSON, E.O. 1977. Weaver ants. Scientific American 237: 146-154.

1983. The evolution of communal nest-weaving in ants. American Scientist 71: 490-499.

1990. 'The ants'. (The Belknap Press of Harvard University Press: Cambridge).

KOHOUT, R.J. & TAYLOR, R.W. 1990. Notes on Australian ants of the genus *Polyrhachis* Fr.Smith, with a synoptic list of the species (Hymenoptera: Formicidae: Formicinae). Memoirs of the Queensland Museum 28: 509-522.

MASCHWITZ, U., DUMPERT, K., BOTZ, T. & ROHE, W. 1991. A silk-weaving Dolichoderine ant in a Malayan rain forest. Insectes Sociaux 38: 307-316.

OFER, J. 1970. *Polyrhachis simplex* the weaver ant of Israel. Insectes Sociaux 17: 49-81.

PEETERS, C. & ANDERSEN, A.N. 1989. Cooperation between dealate queens during colony foundation in the green tree ant, *Oecophylla smaragdina*. Psyche 96: 39-44.

WHEELER, W.M. 1915. On the presence and absence of cocoons among ants, the nest-spinning habits of the larvae and the significance of the black cocoons among certain Australian species. Annals of the Entomological Society of America 8: 323-342.

YAMAUCHI, K., ITO, Y., KINOMURA, K. & TAKAMINE, H. 1987. Polycalcic colonies of the weaver ant *Polyrhachis dives*. Kontyu 55: 410-420.